Role of Plant Growth Regulators in Abiotic Stress Tolerance

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Abstract

Endogenous plant growth regulators play an important role in regulating plant responses to abiotic stress by sensitizing growth and developmental processes. While the physiological and molecular mechanisms linked to the role of ABA and cytokinins in stress tolerance are well explained, there is growing interest to elucidate the associations of auxins, ethylene, gibberellins, brassinosteroids, and polyamines in stress tolerance mechanism and also on possible cross talk mechanism among different growth regulators during stress tolerance acquisition. Identification and characterization of the gene regulating synthesis of different endogenous growth regulators and recent progresses on hormonal signaling, mutant research, and physiological actions have provided scope for manipulating their biosynthetic pathways for developing transgenic crop plants with enhanced abiotic stress tolerance. Researches have also provided some leads in exploiting the potential of growth regulators in enhancing the resistance to abiotic stresses of crops.

2.1 Introduction

Plant growth and productivity are adversely affected by various abiotic stresses. Plants are frequently exposed to a plethora of stress conditions such as low temperature, salt, drought, flooding, heat, and oxidative stress. Various anthropogenic activities have accentuated the existing stress factors. All these stress factors prevent them from reaching their full genetic potential and limit the crop productivity. In the event of growing concerns of uncertainties in climatic conditions, the abiotic stresses have become the major threat to agriculture production worldwide (Bray et al. 2000). The plant responses to abiotic stress condition are believed to be complex in nature as these are the reflections of integration of stress effects and responses at various levels of plant organization. To provide tolerance against stresses, plants are equipped with several

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inbuilt physiological and biochemical mechanisms occurring at cellular level. An understanding of processes linked to these mechanisms is vital in optimizing the crop growth and productivity under stress conditions.

One of the important and widely discussed aspects in abiotic stress tolerance is the regulatory roles of plant growth regulators (PGR). PGR are chemical substances that profoundly influence the growth and differentiation of plant cells, tissues, and organs and also function as chemical messengers for intercellular communication. Their biosynthesis within plant tissues is not always localized. In general, there are five major classes of PGR, and each is grouped together into one of these classes based on their structural similarities and physiological responses. These include the auxins and gibberellins that stimulate predominantly cell elongation; cytokinins, the purine bases that stimulate cell division; ethylene, the olefinic gaseous molecule that regulates among other plant event fruit ripening; and abscisic acid (ABA), the sesquiterpene that regulates senescence and abscission of plant parts and helps in maintenance of plant water relations. Besides these five classes of naturally existing PGR, the steroid hormones brassinosteroids and polyamines are also reported to exhibit growth-regulating activities in plants and are the topics of extensive researches. While these natural PGR are distinctive both in chemical characteristics and in exhibiting characteristic responses, each of the PGR has the potential to alter almost all the aspects of plant growth and development to confer stress tolerance. It is documented that the induction in stress tolerance is induced by the manipulations in the concentrations of endogenous PGR under stress conditions by helping plants in many ways. Most of the progresses made in the PGR research especially on plant adaptation to abiotic stresses are the outcome of advances made in the precise analysis of PGR employing powerful and reliable physiochemical techniques as well advances made in molecular and genetic approaches. Besides the naturally occurring PGR, a wide range of chemicals with well-defined growth regulatory activities have been synthesized, and

several of these have been depicted to have wide applications in improving plant growth and yield and quality of produce. Good progress is also achieved in demonstrating the potential of such PGR in the amelioration of abiotic stress responses in a number of crop plants. In the present chapter, an insight into various physiological and biochemical aspects of PGR in relation to their involvement in abiotic stress is provided.

2.2   Abscisic Acid (ABA)

The ABA is an important chemical signal of plant responses to a range of abiotic stresses, including drought and salinity (Keskin et al. 2010; Verslues and Bray 2006). A dynamic balance between its biosynthesis and degradation, sensitized by developmental and environmental factors, determines the amount of available ABA (Cutler and Krochko 1999). The functions of ABA in plants are multiple. High cellular ABA facilitate modifications in stomatal functioning, root hydraulic conductivity, photosynthesis, biomass allocation between roots and shoots, plant water relations, osmolyte production, and synthesis of stress-responsive proteins and genes to confer stress tolerance (Finkelstein et al. 2002, 2008; Hetherington 2001; Kim et al. 2010a; Hoth et al. 2002; Seki et al. 2002). From the experiments involving radio-labeled ^{18}O, molecular genetic analysis of auxotrophs, and biochemical studies, the pathways for ABA biosynthesis are identified. ABA is biosynthesized in cytosol through the carotenoid biosynthetic pathway (Milborrow 2001). ABA is biosynthesized from the C15 compound, farnesyl pyrophosphate, and a C40 carotenoid, involving isopentenyl pyrophosphate (IPP). IPP is synthesized from mevalonic acid in the cytosol, whereas in plastids, 1-deoxy-D-xylulose-5-phosphate (DXP) from pyruvate and glyceraldehyde-3-phosphate are involved in carotenoid biosynthesis. IPP is converted to a C20 product, geranylgeranyl pyrophosphate, which is further converted to C40 carotenoid, phytoene. The phytoene via series of reaction intermediates like violaxanthin, neoxanthin, and xanthoxin

involving cyclization and hydroxylation reactions is converted to ABA (Nambara and Marion-Poll 2005). The plants under stress show inductions in the activities of enzymes associated with the ABA biosynthesis and relative induction in mRNA leading to ABA accumulations. Besides the inhibition of ABA catabolism under stress is also a factor for induced ABA accumulation (Jia and Zhang 1997). The ABA levels in plants are regulated by its degradation irreversibly into its hydroxylated products like phaseic acid (PA) and dihydrophaseic acid (DPA) (Zhou et al. 2004) or reversibly into the physiologically inactive derivative of glucose ester by glucosidase (Boyer and Zeevaart 1982). It is documented that the PA and DPA contents increase parallel to ABA under stress conditions. However, their levels under stress increase even after ABA content reaches plateau. In contrast upon rehydration of plants, the ABA level shows a decrease, but PA or DPA levels either increase or remain unaltered (Zhou et al. 2004).

Drought and salinity induce ABA accumulation in the leaves of many plant species (Benson et al. 1988; Bray 1988; Pekic et al. 1995; Luo et al. 1992; La Rosa et al. 1985, 1987; Jiang and Zhang 2002; Nayyar et al. 2005; Conti et al. 1994; Upreti et al. 1997, 1998, 2000; Upreti and Murti 2004a, 2005; Satisha et al. 2005). The stress release reverses ABA increase and brings back its levels to prestressed levels. The increases in ABA enable plants to restrict their water loss through transpiration following closure of stomata and enhanced plant water status following increased root hydraulic conductivity (Thompson et al. 2007). ABA also participates in the communication between the root and aboveground part, either by stomatal closure or metabolic changes and gene expression (Zhang et al. 2006; Sobeih et al. 2004). However, such regulatory mechanism is more linked to soil moisture content rather to the leaf water status, indicating that ABA acts as chemical signal produced by stressed roots (Davies and Zhang 1991). The sensitivity of stomata to ABA varies in plant species and cultivars and is dependent upon leaf age, climatic factors like temperature

and relative humidity, plant nutritional status, ionic status of xylem sap, and leaf water status (Dodd et al. 1996). Such variations in ABA for stomatal response are possibly the consequence of variations in the magnitude of ABA transportation to the active site at guard cell. Tardieu and Simonneau (1998) demonstrated that the xylem ABA concentration and stomatal conductance are linearly inverse related and the slope of relationship varied diurnally. Exogenous application of ABA is effective to increase plant adaptive response to various stress conditions (Marcinska et al. 2013; Javid et al. 2011). However, in some cases, exogenous application of ABA did not increase stress tolerance (Chen and Gusta 1983; Robertson et al. 1987), and this nonresponsive condition to ABA is due to lack of ABA uptake or its degradation by microbes.

The stomata aperture is regulated by turgor potential of its surrounding cells. The guard cell volume is actively responsive to signals produced under stress in order to regulate CO_2 efflux for photosynthesis and transpirational water loss. The ABA increase in guard cells reduces plant water loss through transpiration by promoting stomatal closure (Harris and Outlaw 1991). The influx or efflux of K^+ balanced by flux of anions regulates guard cell volume and this process is ABA regulated (Hetherington and Quatrano 1991). Such results are supported from the studies of MacRobbie (1991); externally applied ABA evokes the efflux of K^+ and anion from guard cells. Besides, efforts are also made toward deciphering electrical responses triggered by ABA in the plasmalemma of the guard cells (Blatt and Thiel 1993; MacRobbie 1991). The cellular electrical changes induced by ABA are the outcome of the depolarization effect which reflects a net influx of cations (Thiel et al. 1992). The depolarization is the driving force for K^+ efflux through outward K^+ channel. Besides, Ca^{+2} also plays an important role in ABA-mediated stomata closure. Ca^{+2} participate as intracellular secondary messenger in mediating the ABA effects on stomatal aperture and/or plasma membrane channel. ABA also evokes alkalization of cytoplasm of guard cells (Irving et al. 1992), which is necessary in the

ABA activation of K^+ channel (Blatt and Armstrong 1993). Wilkinson and Davies (1997) demonstrated pH reduction induced by ABA in sensitizing stomata for closure, as guard cells take up ABA more efficiently at acidic pH (Anderson et al. 1994). Recent studies also depict that the ABA closes stomata by involving signal transduction molecule like H_2O_2 (Luan 2002). Likewise, ABA induces production of nitric oxide in guard cells, the increase which negatively regulates ABA signaling in guard cells (Neill et al. 2008). Furthermore, the ABA is also active in root-to-shoot communication in the plants subjected to stress. The ratio between the growth of root and shoot in a plant is sensitive to abiotic stresses, and there is coordination among them via long distance transport of substrates or signal (Munns and Crammer 1996). Passioura and Stirzaker (1993) opined that the ABA acts as a feed-forward signal from the roots to the aerial plant parts under stress conditions. Jackson (1993) provided evidence for influence of the roots on shoot development via transport of hormones in the xylem. Further Saab et al. (1990) stated that the relationship between ABA and root growth is completely different from that in shoots, as higher ABA levels in roots promote root growth at low water potential (Biddington and Dearman 1982; Watts et al. 1981). However, some investigations also reported inhibition in root expansion by exogenous applications of ABA (Cramer and Jones 1996). ABA increase in roots tends to stimulate the water flow by increasing the root hydraulic conductivity and ion uptake, which causes increase in water potential gradient between soil and roots (Glinka and Reinhold 1971). It also increases water absorbing area of roots and helps the plants transport more water and nutrient under stress situations.

Stress conditions in plants induce metabolic alteration resulting in synthesis and/or accumulation of a wide range of proteins (Pareek et al. 1998; Bray 1988; Bartels et al.1996; Cohen and Bray 1990; Piatkowiski et al. 1990; King et al. 1992; Yokota et al. 2002). The identification and characterization of proteins provide an insight into the complexity of stress response

and stress tolerance mechanism (Borkird et al. 1991). Studies have shown the activation of some proteins by drought and salinity stress as well as by ABA. Such information helped in describing ABA involvement in cellular signaling processes in plant-stress interactions (Chandler and Roberstson 1994). Some of the proteins associated with protection of cellular structures are LEA proteins, dehydrin, lipid transfer proteins, desaturase, RAB (responsive to ABA) saturase enzymes, etc. LEA proteins, which are nonenzymatic, and hydrophilic globular proteins are extensively characterized and perform protective functions (Ingram and Bartels 1996; Cushman and Bohnert 2000; Ouvrard et al. 1996; Ismail et al. 1999). Synthesis of ABA is the common dominant factor in the induction of all these proteins and the requirement which is shown through the use of mutants. The ABA-deficient mutant of tomato shows no distinct ABA-responsive proteins when subjected to drought stress compared to the wild type (Bray 1988). ABA treatment to *flacca* resulted in the synthesis of polypeptides similar to the wild type. The stress-responsive proteins have been thought to function in detoxification of cell damage during dehydration (Bartels and Sankar 2005).

A number of genes that respond to stress at transcriptional level have been found to be induced by ABA (Skriver and Mundy 1990; Delasny et al. 1994). However, not all the genes induced by stress are responsive to ABA. There exists ABA-dependent and ABA-independent signal transduction cascade between initial signal of stress and expression for specific gene. Gene expressed during stress helps in protecting cells from stress injury by producing proteins involved in signaling transduction mechanism (Shinozaki and Yamaguchi-Shinozaki 1997). Further, the interaction between transcription factors and their cis-regulatory elements causes expression of stress-inducible genes. Major transcription factor families, which are involved in the regulation of abiotic stress responses, are bZIP, MYB, MYC, NAC, ERF, and DREB/CBF. The ABRE-binding (AREB) proteins or ABRE-binding

factors (ABFs) encode bZIP transcription factors among which AREB1/ABF2, AREB2/ABF4, and ABF3 are induced by dehydration, salinity, or ABA treatment and are involved in enhanced drought stress tolerance (Yoshida et al. 2010). Stomatal closure under stress is induced because of the overexpression of GmbZIP1 transgenic plants, leading to enhanced tolerance to stresses. Members of the bZIP family, like ABP9, are associated with enhanced photosynthetic capacity of plants in drought and heat stresses (Zhang et al. 2008a). Similarly, OsABF1 in roots is involved in abiotic stress responses and ABA signaling (Hossain et al. 2010). In tomato, a bZIP transcription factor SlAREB1 participates in abiotic stress by regulating oxidative-stress-related proteins, LEA proteins, and lipid transfer proteins (Orellana et al. 2010).

The ABA controls abiotic stress signaling, regulated by three components: (1) pyrabactin resistance (PYR)/PYR1-like (PYL)/regulatory component of ABA receptor (RCAR), (2) protein phosphatase 2C (PP2C), and (3) SNF1 (sucrose non-fermenting)-related protein kinase 2 (SnRK2) (Mehrotra et al. 2014). PP2C is a negative regulator of ABA signaling and is similar to ABA insensitive 1(ABI1), ABI2 (homolog to ABI1), and AHG3/PP2CA and hypersensitive to ABA1 (HAB1) (Saez et al. 2004; Yoshida et al. 2006). Gene expression and genetic analysis further indicate a dominant role of ABI1, ABI2, and PP2CA in ABA-signaling pathways in plants. Negative regulation of MAPK (MAPK4 and MAPK6) by PP2C and AP2C1 (Schweighofer et al. 2004) associates PP2Cs with cold and drought stress responses. SnRK2 is a positive regulator of ABA signaling and is identified as ABA-activated protein kinase (AAPK) (Li et al. 2000). The FSnRK2 is the key regulator of plant response to abiotic stress. Phosphorylation at the posttranslational level and gene response to changes under stress regulate SnRK2 expression. Salinity and low temperature stress upregulate expression of SnRK2 genes, while high temperature stress downregulate expression of SnRK2 genes (Huai et al. 2008). Further, Nishimura et al. (2010) showed that overexpression of RCAR1/PYL1, PYL5/

RCAR8, or PYL8/RCAR3 gives more tolerance toward drought stress in *A. thaliana* and interaction of PYR/PYL/RCAR with ABI1 is ABA dependent.

2.3 Cytokinins

Cytokinins are important growth promotory compounds involved in seed germination, morphogenesis, chloroplast biogenesis, maintenance of assimilate mobilization, fruit and leaf abscission, and in the regulation of stomatal functioning and root-to-shoot communication in the plant experiencing stress. These are synthesized primarily in roots (Chen et al. 1985; Binns 1994), besides the shoot apex and other plant tissues. Cytokinins are N^6-substituted adenosine compounds with branched five-carbon side chain (zeatin and isopentenyl adenine). The cytokinins are biosynthesized following two pathways: de novo biosynthetic pathway (Chen and Melitz 1979) and *t*-RNA pathway (Skoog and Armstrong 1970). Most of the biologically active cytokinins are biosynthesized by de novo biosynthetic pathway. The formation of N^6-(Δ^2-isopentenyl) adenosine-5′-mono phosphate from Δ^2-isopentenyl pyrophosphate and adenosine-5-′-monophosphate through catalytic reactions by isopentenyl transferase (ipt) is the important step in cytokinin biosynthesis (Mok and Mok 2001). In the other pathway, *t*-RNA is degraded and isomerized to cis-zeatin by *cis-trans* isomerase (Mok and Mok 2001). The cytokinin levels are regulated through conversions to riboside derivatives and N- and O-linked glycosides derivatives (Brzobohaty et al. 1994; Murti and Upreti 2000; Zazimalova et al. 1999). These derivatives tend to release free cytokinins for developmental events whenever required, by the action of β-glucosidase present in plants. The cytokinins are also catabolized irreversibly by cytokinin oxidases to inactive forms (Brzobohaty et al. 1994). Plants experiencing abiotic stress tend to decline cytokinin concentration (Naqvi 1999; Pospisilova et al. 2000). Upon stress release, the cytokinin restores their normal levels, and response is fast, and species

and cultivar dependent. The cytokinin decline is presumed as the outcome of either reduction in cytokinin biosynthesis or their enhanced degradation or even both. Zhou et al. (2004) reported that the drought stress changes in cytokinins levels in the xylem sap of apple trunk and the changes depended upon drought cycles. During the first cycle of drought and rewatering, cytokinin levels in drought-stressed plants decrease significantly, while in the second, zeatin content declines with no changes in zeatin riboside. During the third cycle, zeatin content did not differ between the treatments. Masia et al. (1994) reported a decrease in cytokinin transport from the root to shoot which occurs during the onset of water stress. Pillay and Beyl (1990) observed reduction in cytokinin concentration in drought-susceptible cultivar of tomato. Upreti et al. (1998) in French bean and (Upreti and Murti 2004a) in onion found profound decline in cytokinins as a result of drought stress with extent of decline dependent upon stress severity, growth stage, and cultivars. Satisha et al. (2005) witnessed a decline in cytokinins in the grape genotypes under soil moisture-deficit conditions. Further, the stress-induced decline in cytokinins depends upon the age of the plant organ, as the young leaves of stressed plants witness greater decline in cytokinins than the old leaves (Upreti and Murti 2004b). Root nodulation is sensitive to drought stress in French bean plants. Upreti and Murti (1999a) reported that the stress-induced decline in root nodulation is linked to decline in cytokinins in roots/nodules. Stoll et al. (2000) in grapevine found that the partial root drying had negative influence on the xylem cytokinin concentration concomitant with distinct increase in xylem-sap pH. Goiocchea et al. (1995) reported decrease in cytokinins in alfalfa under drought, and this was related with accelerated rate of senescence. In desert-grown almond trees, cytokinins showed peak concentrations in the morning and a rapid decrease in the afternoon; these fluctuations preceded daily variation in stomatal conductance (Fusseder et al. 1992). In contrast, Stern et al. (2003) found increased content of zeatin riboside and dihydroxy zeatin riboside in sap with decrease in stem water potential in

water-stressed trees of lychee. In grape rootstocks, NaCl salinity caused reduction in root cytokinins content and the rootstocks with high cytokinin contents under salinity maintained high K-Na ratio and root-shoot dry mass ratio (Upreti and Murti 2010). Vankova et al. (2011) in radish reported that the higher stress sensitivity of radish is associated with higher decline in bioactive cytokinin levels, as a consequence of stimulation in cytokinin regulatory enzymes, cytokinin oxidase.

The ipt is an important cytokinin biosynthesis enzyme, and overexpression of it increases cytokinin levels, leading improvements in stress tolerance. Rivero et al. (2007) and Peleg et al. (2011) found overexpression of ipt gene under the control of *senescence-associated receptor kinase* (*SARK*; a maturation- and stress-induced promoter) improves the drought tolerance in different plants. Merewitz et al. (2011) showed that the drought tolerance enhancement associated in ipt-expressed transgenic plants is also linked to maintenance of accumulation of several metabolites, particularly amino acids (proline, γ-aminobutyric acid, alanine, and glycine), carbohydrates (sucrose, fructose, maltose, and ribose), and organic acids, involved in the citric acid cycle. The accumulation of these metabolites could contribute to improved tolerance due to their roles in the stress response pathways such as stress signaling, osmotic adjustment, and respiration for energy production. Similarly, the expression of ipt gene under the control of cold inducible (COR15a) (Belintani et al. 2012) and SAG12 (McCabe et al. 2001) or maize ubiquitin (Hu et al. 2005) promoter induce low temperature tolerance in petunia and chrysanthemum (Khodakovskaya 2005) and lettuce (McCabe et al. 2001). The ipt gene overexpressed plants also trigger tolerance to stress by expression of ROS scavenging enzymes (Gashaw 2014). There are reports relating increased abiotic stress resistance at low cytokinin levels employing mutants lacking the functional cytokinin receptor (Jeon et al. 2010; Kang et al. 2012). Jeon et al. (2010) showed that the *Arabidopsis histidine kinase* (*AHK*) loss-of-function mutants *ahk2/ahk3* and *ahk3/ahk4* are

more resistant to freezing temperatures than the wild type. Similarly, Kang et al. (2012) showed that all *ahk* mutants possess enhanced resistance to dehydration.

Stomata play an important role in the control of water transpiration and gas exchange in plant leaves, and cytokinins are important in keeping stomata open by regulating ABA action (Veselova et al. 2006). Brault and Maldiney (1999) depict that the cytokinins act at plasma membrane in association with other signaling molecules, as cytokinins antagonize many physiological processes like stomatal closure, leaf senescence, and leaf expansion mediated by ABA (Cowan et al. 1999). Such antagonistic relationship between ABA and cytokinins is possible because metabolically cytokinins and ABA share partially the common biosynthetic pathway. This is supported from the observation that the cytokinins increase stomatal aperture and transpiration rate in plants, the responses opposite to that of ABA (Pospisilova et al. 2000). The cytokinins are also expected to override the effects of ABA on stomata (Pospisilova et al. 2000; Blackman and Davies 1983), and thus reduction in cytokinins under stress condition enhances shoot responses to increasing concentrations of ABA. This led to conceptualizing the cytokinins to act as negative signals in plants experiencing stress. Nishiyama et al. (2011) and Wang et al. (2011) also hinted at possibility of cross talk between ABA and cytokinins, as altered ABA sensitivity in plants modifies cytokinins levels and signaling. Further, the mechanism of cytokinin action on guard cell involves membrane hyperpolarization by stimulation of adenylate cyclase activity, leading to increase in intracellular adenosine $3',5'$-cyclic monophosphate content, stimulation of guanylate cyclase activity, or interaction with a calcium calmodulin system (Pospisilova and Dodd 2005; Incoll et al. 1990). Stomatal opening is also regulated by hydraulic as well as chemical signals (Whitehead 1998). Both naturally occurring and synthetic cytokinins increase transpiration rate and increase in stomatal aperture (Incoll et al. 1990; Incoll and Jewer 1987). The stomatal responses of cytokinins are found variable.

Blackman and Davies (1983) revealed that zeatin alone did not affect stomatal opening, but partially reverse ABA-induced stomatal closure. In contrast, zeatin riboside or kinetin decreased stomatal opening and had no effect on ABA-induced stomatal closure.

2.4   Gibberellins

Gibberellins are tetracyclic diterpenoid carboxylic acid, which influence growth and various developmental processes, such as elongation, germination, dormancy, flowering, sex expression, enzyme induction, and leaf and fruit senescence. The predominant bioactive forms of gibberellins are GA_1 and GA_4 (Sponsel and Hedden 2004). Gibberellins are biosynthesized from trans-geranylgeranyl diphosphate, formed in plastids via the methyl erythritol phosphate pathway (Kasahara et al. 2002) by the action of terpene cyclases, followed by oxidation by cytochrome P450 monooxygenases and then by soluble 2-oxoglutarate-dependent dioxygenases (Hedden and Thomas 2012; Yamaguchi 2008). The dioxygenases are GA_{20}-oxidase (GA20ox), GA_2-oxidase (GA2ox), and GA_3-oxidase (GA3ox) enzymes, and these help in gibberellin metabolism and function to maintain gibberellin balance during growth. The GA2ox genes are most responsive to developmental events as well as to abiotic stress. Most of the information on the role of gibberellins in stress tolerance mostly came from the results of applications of chemical growth retardants used to control growth of crops and have been shown to enhance drought tolerance (Halevy and Kessler 1963). The primary mechanism by which these chemicals exert influence is through inhibition of the biosynthesis of gibberellins (Rademacher 2000) and application of gibberellin to retardant-treated plants and to GA-deficient mutants (Gilley and Fletcher 1998; Vettakkorumakankav et al. 1999).

There are less number of studies on gibberellin and plant responses to abiotic stress. Radi et al. (2006) showed that the presoaking wheat seeds in gibberellic acid increased the

germination potential especially at moderate salinization levels. Between gibberellin levels and the acquisition of stress protection, an intimate relationship exists (Vettakkorumakankav et al. 1999). In sugarcane, supplementing GA_3 as foliar application plays an important role on imparting salt tolerance in terms of enhancing nutrient uptake, as well as the morphological and physiological aspects (Shomeili et al. 2011). Ashraf et al. (2002) showed that GA_3 application increased the nutrient uptake, plant height, leaf area, and yield of wheat under saline conditions. Evidence also shows the involvement of GA_3 in relieving NaCl-induced growth inhibition in rice (Wen et al. 2010). Starck and Kozinska (1980) found that GA_3 causes more absorption of P and Ca^{2+} and less absorption of Na^+, besides adjusting the ion ratios in bean. Bejaoui (1985) concluded that the exogenously applied GA_3 alleviates salt stress due to activation of enzymes which participate in RNA and protein synthesis. Aloni and Pressman (1980) found interaction between salinity and the GA_3 important in petiole elongation, cellular breakdown, and bolting in celery. Maggio et al. (2010) reported that GA_3 treatment in tomato reduced stomatal resistance and enhanced plant water use at low salinity. Likewise, GA_3-priming increases grain yield due to the GA_3-priming-induced modulation of ion uptake and partitioning (within the shoots and roots) as well as hormone homeostasis under saline conditions (Iqbal and Ashraf 2013). Kumar and Singh (1996) witnessed that the seed germination is improved by GA_3 application under saline conditions. The precise mechanisms by which gibberellin is linked to stress tolerance are less understood. One possible mechanism is via its possible interactions with other phytohormones. In this context, the auxin is expected to promote GA biosynthesis (Wolbang et al. 2004). Similarly, gibberellic acid application enhances the catabolism of ABA (Gonai et al. 2004). Application of paclobutrazol, a gibberellin biosynthesis inhibitor, induced stress protection, and application of GA_3 to the dwarf

phenotype reversed the inherent stress tolerance. Reversal of the dwarf phenotype by specific gibberellins suggests that the conversion of GA_{20} to GA_1 and GA_9 to GA_4 is compromised, indicating that the modulation of specific gibberellins plays an important role in stress protection. Sankhla et al. (1989) described that the soil drenching treatment of paclobutrazol is important in minimizing water stress injuries in the fruits of ber trees, while Still and Pill (2003) found that foliar applications or seed priming with paclobutrazol is effective in improving drought tolerance in tomato seedlings. Likewise paclobutrazol improves plant water status in apple (Swietlik and Miller 1983), strawberry (Navarro et al. 2007), and peach (George and Nissen 1992) under drought conditions. Upreti and Murti (2000) documented seed priming with mepiquat chloride effective in offering good germination in beans under osmotic stress conditions. Similarly, gibberellins play an important role in submergence tolerance of aquatic plants, and effect is mediated through the regulation of ethylene and ABA biosynthesis. The ethylene production under submergence conditions promotes gibberellin synthesis and inhibits ABA synthesis for plant acclimation by causing elongation growth (Colebrook et al. 2014). The treatment of rice plants with gibberellic acid during submergence promoted elongation growth and compromised survival, indicating that gibberellin negatively impacts tolerance to prolonged submergence (Das et al. 2005). Conversely, treatment of non-tolerant cultivars with gibberellin biosynthesis inhibitor, paclobutrazol, restricts underwater elongation and enhanced submergence survival. Further, gibberellin involvement in submergence is through upregulation of the ethylene response factor (ERF) domain proteins SNORKEL1 and SNORKEL2 in response to elongation-induced ethylene accumulation in submerged plants (Hattori et al. 2009) which directly or indirectly leads to increase in bioactive gibberellin levels. Osmotic stress induces changes in gibberellin metabolism, resulting in the stabilization of DELLAs and earlier onset of

endoreduplication. Consequently, this response is absent in mutants with altered gibberellin levels or DELLA activity (Claeys et al. 2012). Zawaski and Busov (2014) following whole-genome microarray, expression, physiological, and transgenic evidences showed that gibberellin catabolism and repressive signaling mediates shoot growth inhibition and physiological adaptation in response to drought. Further drought stress elicits activation of a suite of GA2ox and DELLA encoding genes. The transgenic with upregulated GA 2-oxidase (GA2ox) and DELLA domain proteins showed hypersensitive growth inhibition in response to drought besides displaying greater drought resistance as evident from increase in pigment concentrations and reductions in electrolyte leakage. Comparative transcriptome analysis using whole-genome microarray showed that the GA deficiency and GA insensitivity and drought response share a common region of 684 differentially expressed genes, which suggests that gibberellin metabolism and signaling play a role in plant physiological adaptations in response to alterations in environmental factors. Cold stress directly influences levels of bioactive gibberellins as reflected from increase in expression of three GA2ox genes (Archard et al. 2008). Similarly under salinity stress, six GA2ox genes were shown to be upregulated (Magome et al. 2008). Furthermore, the cold-inducible CBF1/DREB1b protein in *Arabidopsis* imparts freezing tolerance, at least in part by activating the expression of GA2ox genes, which in turn leads to reductions in bioactive gibberellins and suppression of growth (Archard et al. 2008). In *Arabidopsis*, the dwarf and delayed flowering 1 (DDF1) protein, involved in salt stress response, binds to the promoter and activates the GA2ox7 gene (Magome et al. 2008). Archard et al. (2006) showed that mutants with reduced gibberellins content shows enhanced survival under salt stress. Also, the gibberellin signaling participation in mediating growth and stress responses to flooding is shown by Bailey-Serres and Voesenek (2010) based on internodal elongation and plant survival.

2.5 Auxins

Auxins (indole acetic acid, IAA) play essential roles in diverse developmental events like root growth, vascular tissue differentiation, auxiliary bud formation, apical dominance, and flower organ development (Zhao 2010) and respond to abiotic stress. However, little information is available on the relationship between stress and auxins in plants, and the role of auxins in alleviating different stress responses needs better understanding. IAA is mainly synthesized in meristematic tissues through tryptophan-dependent and independent biosynthetic pathways (Zhao et al. 2001). In tryptophan-dependent IAA biosynthetic pathways, indole-3-acetamide (IAM), indole-3-pyruvic acid (IPA), tryptamine (TAM), and indole-3-acetaldoxime (IAOX) are identified as major intermediates. The concentrations and ratios of IAA and IAA derivatives in plant tissues and auxin homeostasis are regulated by its degradation, conjugation to amino acids, and transport. And these processes are sensitive to abiotic stresses in plants. The IAA levels are modified in plant by two possible mechanisms under stress: one by changes in expression of auxin polar transporter gene and the other by inhibitions in polar transport by certain compounds accumulated in response to stress (Potters et al. 2009). Besides, IAA metabolism is also modulated by oxidative degradation of IAA through peroxidases induction under abiotic stress and also reactive oxygen species generated during stress (Kovtun et al. 2000). The salinity stress causes reduction in IAA in rice (Prakash and Prathapasenan 1990). However, gibberellic acid treatment during the salinity stress partly reduced the adverse effect of salinity on IAA levels. Dunlop and Binzel (1996) witnessed significant reduction in the IAA levels of tomato by salinity. Sakhabutdinova et al. (2003) reported a progressive decline in the IAA levels in the root system due to salinity. Afzal et al. (2005) documented exogenous IAA application to seeds prior to sowing alleviates the growth inhibiting effect of salt stress. Likewise, decline

in seed germination with increasing salinity levels is improved by IAA or NAA treatments (Gulnaz et al. 1999; Akbari et al. 2007). High temperature affects reproductive development, leading to decline in yield. Upreti et al. (2012) reported that maintenance of high IAA in the reproductive organs of capsicum cultivars is responsible for lower abscission and high temperature stress tolerance. Cold stress and auxin contents are potentially linked (Fukaki et al. 1996; Wyatt et al. 2002), as cold stress inhibits the root gravity response and also auxin. Shibasaki et al. (2009) suggested that auxin concentrations are regulated by changes in auxin transport in plants under cold stress (Shibasaki et al. 2009). Du et al. (2012) documented that the increased tolerance to cold stress is due to the combined effects of IAA and ABA, as ABA or carotenoid-deficient mutants show reduced IAA content and exhibit increased cold resistance (Du et al. 2013). For abiotic stress response, Du et al. (2012) and Du et al. (2013) found that the change in auxin homeostasis could influence ABA synthesis and that the balance of auxin and ABA homeostasis played a crucial role in diverse stress responses. In this regard, Taniguchi et al. (2010) suggested ABA involvement in hydrotropic root responses through modulation in auxin. Kinoshita et al. (2012) illustrated involvement of IAR3 (IAA-Ala Resistant3) in drought tolerance through the production of lateral roots, as IAR3 is effective in producing free auxin by hydrolyzing inactive auxin amino conjugates. Similarly flooding stress negatively affects root development by resisting oxygen supply. Plant tends to develop adventitious roots in response to flooding to alleviate negative effects of flooding stress on plant growth and development. Accumulation of auxins triggers ethylene production, which induces adventitious rooting at the base of the stem (Vidoz et al. 2010). In a study, Muday et al. (2012) reported cross talk between ethylene and auxins in waterlogged plants contributing to the formation adventitious root formation.

Molecular genetic studies made in understanding mechanism of auxin action showed that many auxin-responsive genes are also responsive to cold stress (Jain and Khurana 2009). This is supported from auxin signaling mutants *axr1* and *tir1*, which showed reduced gravity response and responded to cold treatment similar to the wild type (Shibasaki et al. 2009). Likewise, PIN3, an auxin transporter that has been suggested to mediate the early phase of the root gravity response, is inhibited by cold stress (Shibasaki et al. 2009), suggesting that cold stress may affect auxin transport. From transcript analysis, Jain and Khurana (2009) found that many auxin-responsive genes are responsive to cold stress. Du et al. (2012) found that the *OsGH3-2* overexpression decreased free IAA content. Further Du et al. (2013) reported that ABA or carotenoid-deficient mutants have reduced IAA content and exhibit increased cold resistance. PIN proteins associated with auxin transport play an important role in drought tolerance. *OSPIN3T* gene encodes for auxin efflux carrier protein (Zhang et al. 2012) and plays a crucial role in drought tolerance by regulating root and shoot development. Similarly phototropin1, a protein kinase PINOID, is responsible for PIN phosphorylation and is capable of improving drought tolerance at seedling stage (Galen et al. 2007). Besides, several transgenic plants (*PDS-RNAi* transgenic rice, *OsGH3-2* overexpressing rice, *AtYUCCA6* overexpressing *Arabidopsis* plants, and *AtYUCCA6* overexpressing potato plants) with altered IAA level exhibit auxin-related developmental phenotypes together with affected drought stress resistance (Du et al.2012, 2013; Kim et al. 2013). Additionally, endogenous and exogenous auxin positively modulated the expression levels of many abiotic stress-related genes (*RAB18*, *RD22*, *RD29A*, *RD29B*, *DREB2A*, and *DREB2B*) and positively affected reactive oxygen species (ROS) metabolism and underlying antioxidant enzyme activities. Likewise, Cheol Park et al. (2013) showed that the transgenic potato (*Solanum tuberosum* cv. Jowon) overexpressing AtYUC6, members of the YUCCA (YUC) family of flavin-containing monooxygenases, showed high auxin

and enhanced drought-tolerant phenotypes. The overexpression of AtYUC6 in potato establishes enhanced drought tolerance through regulated ROS homeostasis. Under salt stress, Zolla et al. (2010) found a reduction in the increase of lateral roots in auxin signaling mutants, axr1, axr4, and tir and the response depended upon the auxin efflux carrier, PIN2. Sun et al. (2008) documented that salt stress alters auxin efflux carrier, besides inhibiting PIN2 expression. This shows that like cold stress, salt stress interferes with root gravitropism, an adaptive response to reduce the damaging effects of salt stress (Galvan-Ampudia and Testerink 2011). Xu et al. (2012) illustrated that the soil alkalinity increases auxin transport activity mediated by PIN2. Jung and Park (2011) suggested for a possible cross talk between salinity and auxin mediated by transcription factor NTM2 via IAA30 gene during seed germination.

2.6   Ethylene

Ethylene is the simplest olefinic gaseous hormone which regulates a wide range of plant developmental processes such as pollination, seed germination, abscission and senescence, flowering, fruit ripening, root formation, and gravitropism. It is biosynthesized by the conversion of methionine to ethylene via the intermediates, S-adenosyl methionine (SAM) and 1-amino cyclopropane-1-carboxylic acid (ACC) by involving enzymes ACC synthase and ACC oxidase (Yang and Hoffman 1984; Kende 1993). Abiotic stress conditions surge ethylene production by inducing ACC synthase and ACC-oxidase activities. Drought stress enhances ethylene in French bean (Upreti et al. 1998), orange (Ben-Yehoshua and Aloni 1974), avocado (Adato and Gazit 1974), *Vicia faba* (El-Beltagy and Hall 1974), and in many other plant species (Narayana et al. 1991; Guinn 1976; Irigoyen et al. 1992). The increase in ethylene under stress is of adaptive significance as it helps plants to cope up stress by reducing water loss through increased senescence of fruits/leaves and reduced growth. The magnitude of

ethylene increase under stress depends upon growth stage, stress intensity, and stress duration (Upreti et al. 1998, 2000), and higher stress levels tend to reduce ethylene concentration. In pineapple, drought stress has no effect on flower induction and produced significantly less ethylene and had lower ACC-oxidase activity in leaf and stem tissues than the control plants (Min and Bartholomew 2005). Habben et al. (2014) reported that transgenic field-grown plants with downregulated ACC synthase enzyme activity yield higher under drought stress. Salt stress positively influences ethylene biosynthesis, which helps in promoting salt tolerance by enhancing Na/K homeostasis (Lockhart 2013). Yang et al. (2013) illustrated a key role for ethylene in salt tolerance by relating its ability to retain K^+ rather than decreasing Na in roots and shoots. Likewise Jiang et al. (2013) reported that ethylene overproducing (eto1) mutant under salinity exhibits reduced root Na influx and low root stelar and xylem-sap Na concentrations, leading to restricted root-to-shoot delivery of Na^+, along with high xylem-sap K^+ concentrations. Wang et al. (2009) reported that ethylene alters salt tolerance by interfering with other hormone pathways and NO signaling. It also stimulates H^+-ATPase activity to modulate ion homeostasis and salt tolerance. Cold stress alters ethylene levels in plants and the enhanced ethylene level contributes in cold tolerance (Machacckova et al. 1989; Wang and Adams 1982; Ciardi et al. 1997; Zhao et al. 2014). However, tolerance responses of ethylene are variable and species dependent (Kazan 2013). High temperature stress (35/25 °C) in capsicum increased abscission of reproductive organs, which is due to increase in ethylene concentration by accumulation in ACC and induction in ACC-oxidase activity in flower buds and flowers (Upreti et al. 2012). Shi et al. (2012) reported that in vitro-grown *Arabidopsis* seedlings treated with the ACC and mutant overproducing ethylene, eto1, show reduced freezing tolerance, in contrast to increased freezing tolerance by aminoethoxyvinylglycine (AVG), an ACC biosynthesis inhibitor. Zhao et al. (2009) in tomato suggested positive relationship between ethylene

and freezing tolerance from the negative effects of 1-methyl cyclopropene, an ethylene biosynthesis inhibitor on freezing tolerance. Further support for ethylene in cold tolerance is evident from the study of Lockhart (2013) that the ethylene biosynthesis inhibitor 1-methyl cyclopropene (1-MCP) reduces cold tolerance in tomato, whereas ethephon enhances cold tolerance in tomato. Ethylene is also considered important in plant's adaptation to flooding. Under flooding, the lack of oxygen in flooded roots triggers the ACC synthesis, which upon transportation upward in the plants gets oxidized to ethylene to cause nastic movements of the leaves and promote aerenchyma formation (Moore et al. 1998; Colmer 2003). The biochemical mechanism that provokes ethylene biosynthesis under stress is still not clearly understood, and some reports also show variations in ethylene responses. Naylor (1972) suggested greater availability of methionine as a result of increased rate of protein breakdown under stress which leads to the elevated ethylene levels. Beltrano et al. (1997) revealed that the increased production of free radicals under water stress facilitates greater conversion of ACC to ethylene. The increase in ethylene in response to stress is depicted primarily by an increased synthesis of ACC (Yang and Hoffman 1984). Xu and Qi (1993) reported that a slowly developing drought did not promote ethylene or altered ACC levels, while rapidly developing drought enhanced both ethylene and ACC levels. Narayana et al. (1991) also reported more ethylene upon rapid loss of water. Beltrano et al. (1997) observed slight changes in ethylene in leaves under moderate or severe stress conditions. Wright (1980) and Hoffman et al. (1983) showed that ABA interacts with ethylene metabolism by regulating the ACC levels.

Ethylene exerts responses through modulation of gene expression function at transcriptional level by ERF (ethylene response factor) by regulating gene expression under abiotic stress conditions (Zhang et al. 2008b; Hussain et al. 2011). Investigations have suggested the potential of ERF proteins to specifically bind not only to GCC box but also to the DRE/CRT motif, also known as a cis-acting element that

responds to cold or osmotic stress (Lee et al. 2004; Wang et al. 2004). DREB proteins are important ERF, widely studied in abiotic stress responses. The members of the DREB1/CBF subfamily are induced in response to cold stress and improve tolerance to freezing (Liu et al. 1998; Kasuga et al. 1999). Gilmour et al. (2004) reported that the constitutive expression of *DREB1A* and *DREB1B* induces the expression of cold-regulated genes and increases the freezing tolerance. Similar results are observed for the constitutive action of the protein *DREB2*, under conditions of dehydration and high salinity stresses (Liu et al. 1998; Sakuma et al. 2006). A number of cold-inducible genes, such as LEA proteins and enzymes for sugar metabolism and fatty acid synthesis (Fowler and Thomashow 2002), are also upregulated ectopically expressing *DREB1/CBF* members. Trujillo et al. (2008) found that the *SodERF3* is another ERF that is responsible for improved drought and salt tolerance. Likewise Zhang et al. (2009) illustrated that the transgenic plants overexpressing *GmERF3* exhibited tolerance to high salinity and drought stresses, suggesting its crucial role in both abiotic stresses. Similarly, in ERF-VII genes are involved in the response to submergence and hypoxia (Hattori et al. 2009; Hinz et al. 2010; Licausi et al. 2010). Gibbs et al. (2011) and Licausi et al. (2011) suggested that the constitutive ERF-VII factors, like RAP2.12, act as primary trigger for the oxygen deficiency responses. Xu et al. (2006) reported that the SUB1A promotes a quiescent strategy that allows carbohydrate saving and improves tolerance after flooding stress (Xu et al. 2006). Sl-ERF.B.3 (*Solanum lycopersicum* ethylene response factor B.3) gene encodes for a tomato transcription factor of the ERF (ethylene responsive factor) family, which is induced by cold, heat, and flooding, but is downregulated by salinity and drought (Klay et al. 2014). Xu et al. (2006) found that the *SUB1A-1* allele induces the negative regulation of ethylene, making plants able to survive complete submergence for prolonged periods. Besides providing anoxia tolerance, this allele also provides drought and de-submergence tolerance. Similarly, overexpression of the gene *HRE1* shows

increase in anoxia tolerance (Licausi et al. 2010). The ethylene homeostasis during conferring of freezing tolerance seems to be important (Catala et al. 2014), and the 14-3-3 protein, RARE COLD INDUCIBLE 1A (RCI1A), is important in interacting with ACC synthase to modulate freezing tolerance. Hattori et al. (2009) suggested that the ERF transcription factors tends to reduce abscisic acid and gibberellin antagonizing signaling process to support stem elongation and photosynthesis under flooding. Li et al. (2010) showed involvement of TaDi9A, a salt-responsive gene in ethylene signaling. Zhu et al. (2005) reported that the ERF, hos10-1 gene transformed plants, accumulates more Na^+ than wild-type plants but has lower sensitivity to salts, implying salt sensitivity is unrelated to Na^+ accumulation. Archard et al. (2006) found that ACC synthase suppresses the salt sensitivity conferred by NTHK1 in transgenic plants suggesting ethylene is required for counteracting receptor function to improve tolerance.

2.7   Brassinosteroids

Brassinosteroids are polyhydroxylated steroidal phytohormones that are structurally related to animal steroid hormones and possess distinct growth-promoting properties (Bishop and Yokota 2001; Clouse and Sasse 1998). These are considered as phytohormones due to inheriting pleiotropic effects, which influence diverse range of developmental and physiological processes including the promotion of cell elongation and cell division, photomorphogenesis, rhizogenesis, senescence and abscission, xylem differentiation, seed germination, and fruit ripening (Clouse and Sasse 1998; Sasse 1997). Numerous studies indicate brassinosteroid potential in enhancing ability of plant to cope with drought stress, salt stress, and high and low temperature stresses (Fariduddin et al. 2014). The growth regulatory and stress protection capability of brassinosteroids are linked to their action on metabolic processes associated with photosynthesis and nucleic acid and protein biosynthesis (Sasse 1997; Fariduddin et al. 2014). The brassinosteroid biosynthesis is a

two-step pathway involving sterol-specific pathway, squalene to campesterol, and the other, brassinosteroid specific pathway with several conversion steps from campesterol to brassinosteroid involving series of hydroxylation, reduction, epimerization, and oxidation reactions (Agarwal and Gehlot 2000). The C-6 oxidation of castasterone is the final step in brassinosteroid synthesis. The brassinosteroids undergo esterification to form 2,3-glucosyl and acyl conjugates at 3-position of its moiety (Asakawa et al. 1996).

Information on mechanism by which brassinosteroids exhibit stress tolerance is lacking. It is suggested that brassinosteroids regulate stress response by a complex sequence of biochemical reactions, such as activation or suppression of key enzymatic reactions, induction of protein synthesis, and the production of various chemical defense compounds (Bajguz and Hayat 2009). Most of the research on the response action of brassinosteroids to stress factors is made employing their exogenous application. Upreti and Murti (2004c) reported that application of epibrassinolide or homobrassinolide prior to drought stress results in increased root nodulation in French bean, and the response is mediated through induction in cytokinin synthesis and nitrogenase activity. Moreover, epibrassinolide is relatively more effective than homobrassinolide in rendering such response. Kagale et al. (2007) reported improved drought tolerance in B rassica napus seedlings treated with epibrassinolide, and the improved tolerance is due to reduction in reactive oxygen species, induction in antioxidative enzyme activities, and antioxidant contents (Zhang et al. 2008c; Li et al. 2012). Zhang et al. (2008c) also witnessed improvement in photosynthesis by regulating ribulose-1,5-bisphosphate carboxylase/ oxygenase activity and sugar accumulation following brassinosteroid treatment in stressed plants. Rajasekaran and Blake (1999) found delay in stomatal closure induced by drought stress following homobrassinolide treatments. Brassinosteroids are also found effective in modulating salinity stress as evident from improvements in plant tolerance by epibrassinolide treatment. The effect is due to

protective action against stress-induced oxidative damage of membrane lipids and induction in antioxidant enzymes (Ozdemir et al. 2004; Ali et al. 2007; Hayat et al. 2010). Similarly, Ding et al. (2012) witnessed improvement in salt tolerance by epibrassinolide in eggplant. Molecular studies reveal redox-sensitive protein NPR1 as possible critical component of brassinosteroid-mediated enhancement in salt tolerance (Divi et al. 2010). Some studies also show induction in high temperature tolerance by brassinosteroids. Singh and Shono (2005) found epibrassinolide-treated tomato plants as more tolerant to high temperature than untreated plants as a result of high accumulation of heat shock proteins and improvement in photosynthetic efficiency. Similarly, epibrassinolide treatment to tomato plants prior to high temperature exposure protects rubisco enzyme and RuBP regeneration under heat stress in order to provide better protection against high temperature stress (Ogweno et al. 2008). Chilling tolerance in plants is influenced by brassinosteroids. The report of Huang et al. (2006) showed that epibrassinolide application upregulated 17 proteins which were downregulated by chilling to confer chilling tolerance. Chilling tolerance is also attributed to increase in membrane permeability (Janeczko et al. 2007), high pigment accumulation, and upregulation in cold-related genes (Kagale et al. 2007) besides high activation of rubisco and expression of photosynthetic genes (Xia et al. 2009). Thus, the physiological responses of brassinosteroids though are variable due to complexities in the molecular mechanism of their action; their potential in improving abiotic stress tolerance has immense utility in managing plant responses to stress. For widening the scope in this area and effectively harnessing the benefits from brassinosteroid research, more investigations are needed on mechanisms by which brassinosteroids confer stress tolerance.

2.8 Polyamines

Polyamines are important growth regulatory polycationic molecules known to be involved in a wide range of developmental events including organogenesis, embryogenesis, floral initiation and development, senescence, fruit development and ripening, and root development (Galston et al. 1997; Kumar et al. 1997). These are biosynthesized by decarboxylation of amino acids, ornithine, or arginine in the reaction catalyzed by enzymes ornithine decarboxylase (ODC) and arginine decarboxylase (ADC), leading to the formation of putrescine, which by subsequent additions of aminopropyl moiety produces spermidine and spermine, respectively. These reactions are catalyzed by enzymes, spermidine synthase, and spermine synthase. The aminopropyl moiety is formed from decarboxylation of SAM employing enzyme SAM decarboxylase. The dynamics of polyamines metabolism is complex due to coexistence of degradation and conjugation pathways of transport and uptake mechanisms (Martin-Tanguy 2001; Federico and Angelini 1991). Molecular studies reveal that the polyamines are involved in signal transduction pathway through effects on calcium fluxes (Thomas et al. 1993) and interaction with certain transcriptional factors (Wang et al. 1999) and protein kinases (Datta et al. 1987). Further, polyamines and ethylene synthesis are co-linked through sharing of common precursor SAM, and thus these tend to inhibit each other's biosynthesis and action (Tiburico et al. 1997). Polyamines are also found to play an important role in conferring tolerance against drought, salinity, flooding, heat stress, and chilling stress in plants (Gill and Tuteja 2010), as evident from polyamine changes under stress alleviation responses of exogenous applied polyamines (Gill and Tuteja 2010) and transgenic studies in plants overexpressing polyamine biosynthetic gene encoding for enzymes, arginine decarboxylase (ADC), ornithine decarboxylase (ODC), S-adenosylmethionine decarboxylase (SAMDC), or Spd synthase (SPDS) (Liu et al. 2007). The stress-induced increase in polyamines is a reflection of upward regulation of enzymes associated with their biosynthesis and release from polyamine conjugates (Gupta et al. 2013). In general, plants experiencing abiotic stresses tend to

increase polyamine levels, and increase in polyamines helps in the regulation of plant tolerance to stress. The stress-induced increases in polyamine provide tolerance by stabilizing membrane integrity and functionality, altering hormonal balances and inducing antioxidant enzymes. Generally, a polyamine response due to stress depends on species, besides type and concentration of polyamines (Ali et al. 2009). Salt-tolerant barley (Liu et al. 2006) and rice (Krishnamurthy and Bhagwat 1989) cultivars drastically accumulate high levels of spermidine and spermine, with a relative decline in putrescine. Mutlu and Bozcuk (2007) found increase in spermidine content in leaf tissues of sunflower plants, with decrease or no significant changes in other polyamines. Similarly, Zapata et al. (2004) studied effects of salinity on polyamines in varied plant species like *Spinacia oleracea*, *Lactuca sativa*, *Cucumis melo*, *Capsicum annum*, *Brassica oleracea*, *Beta vulgaris*, and *Lycopersicon esculentum* and found that the polyamine titer is greatly altered by salinity with distinct increase in spermidine and spermine contents. Duan et al. (2008) witnessed an increase in enzyme arginine decarboxylase, ornithine decarboxylase, SAM decarboxylase, and diamine oxidase activities, as well as free spermidine and spermine and soluble-conjugated and insoluble-bound putrescine, spermidine, and spermine contents in the roots of cucumber cultivars following salinity stress. Wei et al. (2007) studied the effect of salt stress on polyamine contents in leaves of *Solanum melongena*-grafted plants employing salt-tolerant *Solanum torvum* as rootstock. The increase in the contents of free, soluble-conjugated, and insoluble-bound polyamines, with considerable decline in diamine oxidase and polyamine oxidase activities, was observed. The polyamine increase in grafted plants protects the grafted plants against salt stress by triggering higher activities of antioxidant enzymes like superoxide dismutase, peroxidase, and ascorbate peroxidase and glutathione reductase enzymes. Kim et al. (2010b) reported a decrease in spermidine but an increase in spermine under salinity in Chinese cabbage. Likewise Reggiani

et al. (1994) reported an increase in spermidine and spermine but decreased putrescine contents in plants under NaCl stress. Zhao et al. (2003) witnessed salinity dose-dependent increase in polyamines and reduction in bound polyamine fraction and concluded that the plant growth and ratio of bound and free polyamine contents are positively related. Upreti and Murti (2010) found significant alterations in root polyamines in grape rootstocks by salinity stress with tolerant rootstock showing greater increases in spermidine and spermine as well as ABA. The high increase in polyamine helped plants in maintaining high root-shoot biomass ratio and high K-Na ratio in the tolerant rootstock. Similarly, Anjum (2008) reported that citrus rootstock, Cleopatra mandarin, shows better growth and chlorophyll efficiency under salinity stress which accumulated high spermine and carbohydrates but low chloride ions in leaves and roots under salinity. Application of exogenous polyamine is efficient in manipulating the levels of endogenous polyamine during stress, and the stress protection effect is rendered through the maintenance of membrane integrity, regulation of gene expression for the synthesis of osmotically active solutes, reduction in ROS production, and controlling of the accumulation of Na^+ and Cl^- ion in different organs. Anjum (2011) reported that spermidine treatment to NaCl-stressed plants reduced salinity-induced decline in leaf number, chlorophyll content, Fv/Fm, net photosynthetic rate, and N content and reduced Na^+ contents of the plants. Additionally spermidine improved cellular Ca^{2+} and Mg^{2+} contents in salinity-treated plants. In pomegranate plants, putrescine and spermine are effective in reducing the stress-induced decline in growth rate without causing major alteration in Na^+, Cl^-, and K^+ contents of roots and apical and basal leaves (Amry et al. 2011). In addition, the protective role of polyamines against high salt stress is a consequence of altered control of Ca^{2+} allocation through regulating Ca^{2+}-permeable channels, including CAXs (Yamaguchi et al. 2006, 2007). The increase in cytoplasmic Ca^{2+} results in prevention of Na^+/K^+ entry into the cytoplasm, enhancement of Na^+/K^+ influx to

the vacuole and, likewise, the suppression of Na^+/K^+ release from the vacuole. Exogenous polyamine partially reversed the NaCl-induced phenotypic and physiological disturbances in citrus. The effect is due to upregulation of expression of polyamine biosynthesis and catabolism genes, regulation of transcript expression and activities of antioxidant enzymes, and restoration of NO-associated genes, such as NR, NADde, NOS-like, and AOX, along with S-nitrosoglutathione reductase and nitrate reductase activities in the salinity-exposed plants (Tanou et al. 2014). In cucumber seedlings, Shu et al. (2012) found that spermidine alleviates salt-induced damage by regulating the levels of endogenous polyamines and improvement of photochemical efficiency under stress conditions. The reduction in Na content in shoots induced by polyamines is be an effective strategy for combating high salinity. Zhao et al. (2007) found that the polyamines combat deleterious effects of salinity in barley by altering Na and K balance to improve K^+/Na^+ homeostasis, restricting Na^+ influx into roots and by preventing K^+ loss from shoots. Lakra et al. (2006) also demonstrated increase shoot K allocation by salinity. In pistachio seedlings, Kamiab et al. (2014) found spermidine and spermine treatments were effective in improving salinity tolerance by inducing superoxide dismutase and catalase activities and by decreasing the hydrogen peroxide (H_2O_2), thus balancing ions toward lower Na-K ratio. Similarly, drought stress leads to accumulation of free or conjugated polyamines in many plant species, indicating that polyamine biosynthesis plays an important role in plant response to stress (Liu et al. 2007). Upreti and Murti (2005) reported cultivar difference in polyamine content changes in French bean cultivars under drought stress conditions. Moreover, the stress response on individual polyamine varied with stress duration. The putrescine which increased initially with stress declined under severe stress regimes. In contrast, spermidine levels consistently declined and spermine levels progressively increased with stress. The spermine level under stress was related with ABA and stress tolerance of

cultivars. Differential response of drought stress on changes in individual polyamines is also shown by Turner and Stewart (1986). Exogenous polyamine applications have been tried in providing evidence for its role in counteracting stress. The polyamine treatments increased endogenous polyamine levels in plants under stress (Tiburico et al. 1997) and also reversed stress-induced changes in growth and cellular injuries. Spermine application is found effective in improving net photosynthesis rate and water use efficiency in wheat leaves experiencing drought (Farooq et al. 2009). In tomato, spermidine is responsive in improving drought resistance by increasing gas exchange parameters and reducing internal CO_2 concentration by preventing stomatal closure and stimulating CO_2 uptake (Zhang et al. 2010). Evidences indicate the role of polyamine in the modulation of stomata aperture, an effect similar to ABA, by targeting KAT1-like inward K^+ channel in guard cells (Liu et al. 2000). Polyamines are also implicated in plant performance in flooded soil. The accumulation in putrescine in flooded roots stimulated PM ATPase activity, which helps in cell homeostasis and nutrient acquisition (Bertini et al. 1997). Yiu et al. (2009) witnessed alleviation of flood stress in onion by putrescine through reduction in superoxide radicals and H_2O_2 (Yiu et al. 2009). Polyamines are also involved in the regulation of intracellular homeostasis under flooding (Reggiani et al. 1993). The anoxic condition under flooding tends to decrease polyamines in the absence of K^+, but supplementation of K^+ under such conditions reduces negative effect of anoxia on polyamines. Jia et al. (2010) reported that application of spermidine to cucumber roots enhances ATP production and alleviates flooding responses by enhancing aerobic respiration and declining fermentation metabolism. Shi et al. (2009) also observed that the putrescine application is efficient in the alleviation of stress-induced reduction of gas exchange variables of cucumber subjected to root-zone hypoxia by enhancing nitrate reductase activities. Likewise high temperature stress alters polyamine balance, which helps in providing

thermotolerance to plant by stabilizing membrane structural integrity and functionality (Edreva et al. 1998). Such effects are due to the polycationic nature of polyamines which facilitates their strong binding to nucleic acids, proteins, and membranes (Childs et al. 2003). Thermotolerance by polyamines is also possible by regulating heat stress-induced inhibition of photosynthetic efficiency. Upreti et al. (2012) reported that high accumulation in spermidine and spermine in flower buds and flowers of capsicum cultivars is an important attribute of thermotolerance as found by lower decline in abscission of floral parts. The increased polyamine also downregulates ethylene production leading to reduction in abscission of reproductive organs under high temperature. Murkowski (2001) found that the spermidine application improves high temperature tolerance in tomato plants, by lowering thermal damage to the pigment-protein complex structure. Huang et al. (1991) witnessed high temperature-induced accumulation of putrescine at filling stage of rice which helps in thermotolerance by regulating the stress-induced decline in photosynthetic capacity, chlorophyll content, and RuBPC activity. Similarly, exogenous spermine is effective in alleviating heat-induced damage to the photosynthetic apparatus of cucumber by shielding protein complexes in thylakoid against heat damage (Li et al. 2003). Genetic modifications of the polyamine biosynthetic pathway are useful to establish the function of polyamines in plant responses to abiotic stress. The investigations on gene expression associated with polyamines under stress have been made, and reports indicate the presence of complicated transcriptional profiling (Gonzalez de Mejia et al. 2003). The mRNA of some polyamine biosynthetic genes is rapidly induced immediately after stress in some species, and in others it was induced when stress was exerted for a certain period, indicating that the polyamine genes are differentially regulated under stress (Malamberg et al. 1998). The elevated putrescine levels as a result of overexpressing ADC2 induce drought tolerance, which is related to reduction of water loss by the induction of stomata closure (Alcazar et al. 2010). The EMS mutants of *Arabidopsis*

thaliana spe1-1 and spe2-1 displaying reduced ADC activity are deficient in polyamine accumulation after acclimation to high NaCl concentrations and exhibit sensitivity to salt stress (Kasinathan and Wingler 2004). The mutant, adc2-1, showing diminished putrescine content is more sensitive to salt stress, whereas exogenous addition of putrescine protects salt-induced injury in such mutant (Urano et al. 2004). Similarly, spermine-deficient mutants are sensitive to salt, while the addition of spermine suppresses the salt sensitivity, suggesting a protective role of this polyamine to high salinity (Yamaguchi et al. 2006). Alcazar et al. (2010) opined that upregulation of polyamine biosynthetic genes and accumulation of polyamines under stress are ABA-dependent responses as ABA modulates polyamine metabolism at the transcription level by upregulating the expression of ADC2, SPDS1, and SPMS genes under stress conditions. Transcript profiling also revealed that cold enhances the expression of ADC1, ADC2, and SAMDC2 genes (Cuevas et al. 2009).

2.9 Conclusions and Future Perspectives

Plant hormones are vital components of plant growth and development under abiotic stresses. The stress conditions alter their levels which help in plant adaptation through their responses on stomatal functioning, plant water balance, nutrient allocations, and source-sink transitions, besides maintaining antioxidant status. There is either an increase or decrease in the endogenous PGR levels in plants under stress conditions, and responses are cultivars, stress duration, and stress intensity dependent. While stressed plants invariably showed an increase in ABA and decrease in cytokinins, the gibberellins, auxin, ethylene, and polyamine levels show variable responses to abiotic stress factors. Significant progresses have been made over the last few years in understanding processes regulating the biosynthesis and metabolism of naturally present PGR and their associated roles in signaling mechanisms. Besides, PGR often alter gene expression by

inducing or preventing the degradation of transcriptional regulators. Use of mutants with modified hormone biosynthesis pathways is helpful in unfolding mechanism of actions associated with different PGR under stress conditions. The progresses on molecular aspects of hormonal physiology have led identification of genes associated with biosynthesis of different PGR and genes encoding their receptors. And information on stress-induced manipulations in genes has been vital in establishing the role of PGR in adaptation of plant to abiotic stresses. The efforts are also made in manipulating genes for balancing plant-stress responses and in interaction of PGR and other cellular metabolites following stress acquisition. However, most of the studies on hormonal role in stress tolerance are carried out in isolation. As the PGR are interrelated at cellular level synergistic or antagonistic cross talk, and there is overlapping of various stress factors at cellular level at plant level, the mutual interactions and communications between PGR through involvement of unique set of genes are vital to plant responses to different stresses. This aspect needs due emphasis in defining involvement of PGR in plant adaptation to abiotic stresses. The success in elucidating roles of PGR in stress tolerance both at cellular and molecular levels helped in showing positive effects of exogenous application of PGR and their synthetic substitutes and of compounds capable in modifying PGR metabolism in improving stress tolerance in wide range of crop species. However, commercial benefits of such results are yet to be established because of gaps in understanding the physiological basis of their actions. Bacteria and mycorrhiza are efficient in producing PGR and have potential to manipulate their endogenous levels for eliciting growth responses in plants and inducing stress tolerance. Efforts are needed to exploit their benefits as alternate tool in the management of abiotic stresses. Further, the involvement of polyamines and brassinosteroids in the regulation of plant growth and development and stress tolerance in plants is well understood. However, more research is needed in unraveling the mechanism of their stress-protective roles, especially from the point of their interactions and interrelations with other PGR as well as with stress-responsive genes.

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